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Changes of paradigms in agriculture soil microbiology and new challenges in microbial ecology

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A B S T R A C T

At the beginning of the 20th century Louis Pasteur laid the foundations of classical microbiology, based on the cultivation of microorganisms. Microbiology ceased to be an exclusive concern in matters of health or food conservation and extended to almost all fields in Nature. Microbes were recognized as the catalysts of all the cycles of the elements in our planet. In this context, agricultural microbiology works as a catalog of curiosities that offers the possibility to isolate particular microorganism and convert them into modern additives of agriculture. However, this paradigm vanished not many years ago, after a big anomaly in bacterial counts. Biochemical tools allow us to see the new unculturable microbes and a new scenario of soil microbiology is under construction at present. The new concept of microbiome expands the complexity of the soil where any macroscopic form of life develops. Analyzing the soil microbiology at a soil microaggregates scale suggests that agricultural managements are the way of shaping soil microbiomes to improve soil quality and improve crop production and soil services without harming the environment. The integration of soil microbiomes knowledge into the other levels of the soil food web is the future of soil science and could be one of the clues to mitigate the global climate change.

1. Introduction

Soil is one of the biggest reservoirs of biodiversity in our planet. Soil is also the very basic resource to produce food for humans and animals and different materials for very diverse purposes, textile fibers, biofuel, wood and fiber for construction. Most of these materials are originated in different plant species that are cultivated in places where appropriate top soil is available. Soil is a complex living system and is the place where the transformation of matter and the cycle of chemical elements take place. Soil regulates water and air quality and sustains the cycle of elements and transformation of matter. As a consequence of all these services, soil provides benefit to human health (Wall et al., 2015; Rillig et al., 2018).

Soil benefits through agriculture implies the harvest of the plants. This harvest means a kind of extractive activity from soil, as mining does. Along time, soil activity can restore what has been extracted from it but, that restoration capacity is absolutely based and dependent on soil biodiversity. The abuse of soil use drives it into degradation problems and desertification processes. Life in soil is mostly represented by microbes. So, we should understand soil microbiology to do a correct soil use and management in order to preserve the resource for the present and the future.

2. The origin of microbiology

During the 19th century Louis Pasteur laid the foundations of classical microbiology, based on the isolation and cultivation of microorganisms (Raichvarg, 1995). Along time, the study of microbiology ceased to be an exclusive concern in matters of health or food conservation and extended to almost all fields concerning natural products. This is how the soil microbiology paradigm was constructed, in which microorganisms were recognized as the catalysts of all the cycles of the elements in our planet and also the source for all soil-borne pathogen agents for some plant, animal or human diseases.

3. The origin of modern agriculture

The history of farming begun thousands of years ago when human beings changed hunting and gathering to become sedentary and began to cultivate the land and to use tillage as a technique of agriculture production and weed control. From an evolutionary point of view, it is interesting to realize that may had not been the man whom domesticated wheat, but that wheat, as a plant species, domesticated the homo sapiens species (Harari, 2011). In the 19th century, with the arrival of the industrial revolution, mechanical power facilitated soil tillage and agriculture became an important industrial human activity.

Modern agriculture paradigm started as a green revolution by the

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middle of 20th century as a consequence of the conjunction of two independent knowledges. On one side, plant physiology started to define the main statements of plant nutrition based on nutrients requirements as inorganic forms of Carbon, Nitrogen, Phosphorous, Sulfur, Potassium, together with the description of the plant processes of absorption, transportation, assimilation and growth (Raven et al., 2005). On the other side, the developments of chemical detonators and other products aimed for war defense programs gave origin to new products useful in agriculture as fertilizers, herbicides, pesticides, fungicides and antibiotics, significantly enhancing crop production in intensive and extensive forms of practice.

Conventional tillage is a practice in which grooves are drawn from a certain depth on the surface of the soil, from which it loses its original structure and mixes. Tillage has two main objectives: on the one hand the control of the structure, and on the other hand, the incorporation of organic waste in the soil (Balesdent et al., 2000). This technique is often used to encourage the mineralization of organic matter, soften the soil and prepare a suitable area for the seeds, which will be deposited using a planter or manual equipment. Agriculture based on soil tillage has exacerbated the problems of soil degradation due to water and wind, the oxidation of organic matter and a decrease in the arable layer and the structure of soil (Six et al., 1999).

Looking for a solution to the negative effects produced by the conventional tillage, during the middle of the 20th century, an agriculture without tillage was developed with the possibility of diminishing the impact on the soil and the environment. Direct seeding or no-till management arises in response to the erosion problems produced by conventional tillage. With no-till, the soil remains completely imperturbable before sowing except for the small furrow produced to deposit the seed, and where the control of the weeds is done by means of herbicides and other crops (Albertengo et al., 2013). No-till has been recognized as an effective practice to conserve and improve soil quality (Lal, 2004), although it is still a matter of debate. When no-till agriculture is compared to conventional tillage one, it is observed that the former reduces the erosion and the loss of the top soil, increases the organic matter and the carbon stored product of the remains of the crops that remain on the surface (Pandey et al., 2014; West and Post, 2002). Physical properties such as increased water holding capacity, and reducing soil compaction are improved (Derpsch et al., 2010). Another benefit of no-till is the lower costs in terms of fuel for the plow that is not done (Lal, 2004). Studies carried out by several laboratories including ours show that no-till has higher values of carbon, phosphorus and carbon from microbial biomass compared to conventional tillage. At the physical level, no-till presents higher values of aggregates of macroaggregated type. The smaller aggregates are more abundant in conventional tillage. In line with these results, a large variety of studies have shown that tillage breaks macroaggregates in soil (Beare et al., 1994; Jiang et al., 2011a, 2011b; Kandeler et al., 1999; Six et al., 2002). In addition, these chemical and physical aspects are possibly related, since larger aggregates offer greater protection to the organic matter occluded inside them (Christensen, 2001; Franzluebbers and Arshad, 1996). After a huge metadata analysis, Pittelkow et al. (2015) claimed that no-till management per se has a negative impact on crop yield, with a decrease close to 6% mainly in humid regions of the planet. Nevertheless, other authors discussed that no-till managements should be carefully evaluated including other practical components, as crop rotation, in the evaluation of the history of land use to avoid overlooks or misunderstandings (Derpsch et al., 2014). The value of no-till appears when it is combined with other elements that define conservation agriculture. A more recent metadata analysis study, that included other variables besides crop yield, shows the broad benefits of no-till in terms of sustainability of the system (Zhao et al., 2017).

4. Microbes as a particular additive for agriculture

One of the most important discoveries regarding agricultural microbiology, after Pasteur established the basis of culturable microbiology, was the recognition and description of atmospheric-nitrogen fixing bacteria (Hellriegel and Wilfarth, 1888). Those bacteria were responsible for the formation of a new plant organ, the nitrogen fixing root nodule (Beijerink, 1890) in legumes (Doyle, 2011). Being legumes the most important plants in terms of nitrogen fixation, a lot of research has been developed to understand the genetic basis of these symbioses. This knowledge was the basis for the worldwide inoculant production for legume crops. The search for more efficient strains is still a matter of developments in many countries with agriculture-based economies. The possibility to combine in a same diazotrophic bacteria the trait of reduction of N_2O to N_2 opens a new tool for combating the reduction of an important green-house gas in order to revert or control the planet climate change (Mania et al., 2018). Biological nitrogen fixation is still a clue knowledge for sustainable development reducing the need of N fertilizers chemical synthesized by the Haber Bosch process with a huge consumption of fuel energy. Recent plant genomes analyses revealed the basic genetic needs for this biological trait (Griessman et al., 2018; van Velzen et al., 2018) and opened the possibility to transfer it to other important crops as cereals.

Another important discovery, useful for agriculture, happened in the last decades of the 20th century. After the recognition of suppressive soils where plants did not develop soil-borne diseases, it was possible to isolate bacteria from plant rhizosphere with new traits. Those new strains were antagonist to pathogen fungi and/or were able to promote plant growth (Kloepper et al., 1980). Those findings gave origin to the concept of plant growth promoting rhizobacteria, shortly known as PGPR. Since bacteria with similar traits had been isolated from completely different places, bulk soil, inner tissues of the plant, phyllosphera, etc., nowadays this concept is referred as plant benefit bacteria (Glick, 2015). These new group of microbes gave origin to an important industry of biofertilizers that came to agriculture as complementary or replace tools for agrochemicals.

In this context, agricultural microbiology works as a catalog of curiosities that offers new biological additives to agriculture and silviculture that are environmentally friendly. We can mention nitrogen fixers bacteria, either symbiotic or free-living ones; phosphorous, sulphate and K solubilizers and mobilizers; antagonist of pathogens; alleviators of plant abiotic stresses, probiotic bacteria that enhance plant-defense responses (Glick, 2015). Most probably the list will continue growing. Since more than one of these traits can be found in a single bacterial or fungi isolate, it is important to quantify these traits in order to do a good selection of inoculant before the field test (Agaras et al., 2015; Finkel et al., 2017).

5. A great count anomaly and a scientific revolution

The quietness in microbiology science was vanished some years ago after an anomaly found in the lab: an inconsistent comparison of bacterial counts in water samples. In a review by Staley and Konopka (1985) a great discrepancy (two or more orders of magnitude) between the numbers of microbes counted by plate or by direct observation under the microscope was discussed and highlighted an anomaly that was previously suggested in 1932 by Razumov (*in* Staley and Konopka, 1985). Besides different technical aspects that can be used as possible reasons to explain some differences between the final numbers of different counting methods (dead vs alive cells, physiological active cells vs dormant ones, grouped cells in microcolonies vs single cells, differential response of cells to a particular dye or labeled metabolite, etc.), the analyses by Staley and Konopka point out something else than technical problems. Their conclusions suggest the existence of an unculturable population of microbes that was finally discovered everywhere, some years after, when molecular methods based mostly on DNA analyses and massive sequencing techniques became available, and were applied to different samples from very different environments (de Bruijn, 2011). Suddenly, we were less alone in the universe than we

were used to be or supposed to be. The "culturable" microbiology that we know since Pasteur's times constitutes, in the best of the cases, 1% of what exists out in nature, not only in quantitative terms but also qualitatively, regarding its microbial diversity. Everything was changed and we are still trying to understand the new scenario.

The use of different biochemical tools and the development of molecular technologies and the development of bioinformatics made possible massive DNA sequences and consequent analyses of a huge number of samples (de Bruijn, 2011). In that way, the door to the unknown was opened. This new knowledge is driving biological sciences into a new paradigm shift in terms of a scientific revolution by Thomas Kuhn (1962). The new concept of microbiome (Jansson and Hofmockel, 2018) expands the complexity of the scenario where any macroscopic form of life develops. Life suddenly appears in many different places and niches where it was thought to be free of microbes and life (Farias et al., 2013; Lynch et al., 2012).

6. New tools for a new scenario: soil microbiology as part of agriculture

Metagenomics approaches with massive sequencing of soil DNA/RNA of particular genes as ribosomal ones, open the door for a completely new scenario where diversity of bacterial, fungal, archaea and protists can be described in particular environments (Xiong et al., 2017; de Quadros et al., 2012; Dong et al., 2017; Geisen et al., 2018). The description of soil microbiome diversity and structure constitutes a completely new challenge for a novel and awesome vision of life in Earth. The availability of a huge amount of data made possible a geographic description of top-soil microbiomes at a global scale (Ramirez et al., 2018; Barham et al., 2018; Delgado-Baquerizo et al., 2018). Nevertheless, it is worth noting to recognize the many limitations of these techniques, and to be cautious about the inferred conclusions (Prosse, 2015). Not only the description of the microbial diversity structure is important, being able after massive DNA sequencing, but the microbiome functions can be also investigated through the metagenomic approach finding the functional genes present in the microbiome, allowing a description of potential functions od metabolic pathways in soil. Sequencing massive extracted RNA, the transcriptome of the microbiome, could be approached, and the analysis of the soil metabolomics, that is the diversity of molecules present in soil, could be the source information to build a model to understand the biochemical functions expressed in soil, or methaphenome as some authors claimed (Doolittle and Zhaxybayeva, 2010). Indeed, one of the main challenges in soil study would be to reach one step ahead from the microbial diversity structure to the functional structure; in other words: from metagenomics to metaphenomics in soil microbiome (Jansson and Hoffmokel, 2018).

Besides DNA/RNA sequencing techniques, other molecules have been used to describe microbiomes or microbiome functions in soil. Fatty acids profiles from phospholipids (PLFA), or neutral soil lipids fractions (NLFA) have been used to describe microbial community structures (Zelles, 1999). The use of particular fatty acids as indicators of particular microbial taxon is now a matter of debate (Fråstegard et al., 2011) because the approach was originally established from the analyses on culturable bacteria. These limitations laid not to use this molecular approach to describe soil microbiomes in many studies. But, being the soil a complex biological system, the analysis of lipidic signature obtained from whole soil fatty acids appears to be a powerful tool to characterize soil use and management from a systemic point of view of soil structure and function (Ferrari et al., 2018).

The crop yield depends largely on the availability of nutrients in the soil. These nutrients may be either of chemical origin provided by fertilizers or biofertility products obtained after transformation of the organic matter by extracellular enzymes released to the soil by the mesofauna, macrofauna, microbes, and plants (Gianfreda and Rao, 2014). Soil Enzymes activities has been proposed as biological indexes of soil quality, health and biodiversity since they are an expression of soil function (Nannipieri et al., 2012). Alternatively, the microbial activity as a physiological profile can be measured through oxygen consumption curves with different added carbon sources, an approach that made possible the differentiation of soils with different histories of use (Gomez and Garland, 2012).

Soil function depends largely on its physical structure and soil structure is a consequence of the integration of all soil particles and microbes in different sizes and kinds of aggregates as a consequence of microbes-mineral particles interactions. The arrangement of aggregates of different sizes and associated pore networks determines the niches were microbial life and processes occur (Totsche et al., 2018). Besides soil aggregation has been thought to be a biota driven process, it has been historically examined focusing in agricultural practices as tillage and physicochemical soil properties. Very recently, a meta-analysis showed the important contribution of soil biota to soil aggregation, where species interactions across major taxonomic groups are a main contribution factor (Lehmann et al., 2017).

The study of the soil microbiology at a scale according to the microorganism size, i.e. at the level of soil macro ($> 250\,\mu m$)/microaggregates ($< 250\,\mu m$) shows that the diversity and microbial functionality is different according to soil aggregates size (Neumann et al., 2013; Bailey et al., 2013; Hemkemeyer et al., 2018; Bach et al., 2018). Cropping affects bacterial diversity at a microscale suggesting that managements effects should be analyzed at this level of soil structure (Constancias et al., 2013). The fractionation of soils into different size aggregates implies also a technical problem because it is clearly not the same to do dry sieve or water sieve of soils (Bach and Hofmockel, 2014; Schutter and Dick, 2002). As stated before for the DNA analysis, it is important to consider the limitations of the different techniques in order to do an accurate interpretation of the data.

Soil ecosystem services are mostly determined by biotic factors that are shaped by abiotic ones such as the physical and chemical properties of the soil, as well as climatic factors. Abiotic factors regulate the interactions between the soil biota components including the plants, the fauna and the soil microbiomes which can represent about 80% of the soil biomass (Nannipieri et al., 2003). Although extracellular enzymes are clearly important for soil function, the factors regulating enzyme production remain unclear. Enzymatic activities respond to the availability of substrates through changes in microbial activity induced by environmental factors, but those environmental factors are not yet clear (Allison et al., 2011). Organisms recognized as soil engineers, present in the meso- and macro-fauna, are probably clue actors in the shaping of soil microbiomes. Everything is out there waiting for our curiosity to give us new answers. The main concern is to find the right question. For instance, what factors are locally shaping microbiomes in agricultural soils? How can agricultural practices and crop rotations be handled in order to pay attention to the needs for reducing gasses affecting the global climate change and at the same time assuring crop productivity to help supporting the population growth?

7. Microbiology as a diagnosis

Most of the facts described above can be used as a starting point to develop new and more precise or sensitive soil quality indicators (Bünemann et al., 2018). Consequently, soil microbiomes structure related to soil management could be a diagnosis tool (Schmidt et al., 2018; Mbuthia Acosta-MArtinez et al., 2015).

For instance, Argentina is an example of a country that extends its agriculture activity to a very large land surface, covering more than 20 million hectares cultivated under no-till practice (Albertengo et al., 2013). In those soils, the description of soil microbiomes shows a differential structure according to soil use (Monteccia et al., 2015), tillage practice (Carbonetto et al., 2014) or agricultural practice in term of crop rotation under no till, highlighting that monocropping reduce bacterial diversity at the regional level (Figuerola et al., 2015). These

results call for attention on the environmental consequences of using only agrobusiness as the driver for soil management and Farmer's decisions. Moreover, it is possible to find particular bacterial OTUs as indicators of land use (Figuerola et al., 2012; Navarrete et al., 2015).

8. The challenges

The increase in the world population derives in a growing demand for food. This fact has been used for many years as an argument to justify the adoption of non-sustainable ways of doing agriculture, based on an intense use of agrochemicals with unknown consequences for the environment, and lately to the same world population that was the central part of the original statement. Thus, it is essential to adopt agricultural practices compatible with an increase ecosystem services from the soil and crop yield, at the same time, in order to cover production demands, avoiding soil degradation (Foley, 2011).

The ecosystem services lay their fundaments in the living organisms that inhabit the soil, from the plants through the macro-, meso- and micro-fauna to the microbial communities. The different soil managements and uses would modify the chemical and physical parameters of the soil, thus conditioning the structure of the microbial communities that inhabit it. The new challenge is how we can manipulate crop rotation and agricultural practices to manage the soil microbiome to increase soil fertility and improve crop production (Fierer, 2017).

As said before, the main goal in the actual soil studies are dedicated to understand the relation of soil microbiome functions and its structure (Fierer, 2017; Jansson and Hofmockel, 2018). The clue will probably come from a right interpretation of the data generated by the massive sequences of soil DNA and soil RNA in order to connect soil genetics with its expression and final function (Jansson and Hofmockel, 2018). Afterwards, the challenge will be to integrate how different environmental factors as agricultural practices affect the microbiome activity and soil structure.

It is expected that future agricultural practices will be strongly influenced by the new knowledge that is being generated on the soil microbiomes (Liu et al., 2014; Navarrete et al., 2013). Manipulating above ground biodiversity, selecting an appropriate crop rotation and the use of cover crops, according with the possibilities of the particular environment, we would probably help to shape soil microbiomes in the right direction of increasing crop productivity in a sustainable way, using soil services, reducing the use of chemicals and environmental impacts. Through the crop rotation we are manipulating the input of energy into the soil as photosynthates that enter the soil via root structure and root exudates. This energy input is afterwards transformed through plant debris mulch and consequent action of mesofauna, macrofauna and microbiomes (Helming et al., 2018; Bünemann et al., 2018; Finn et al., 2017; Xiong et al., 2017). The raising knowledge on soil microbiomes should be integrated in new research projects that analyze at the same time what happens with the dynamics and diversity of other taxonomic groups belonging to protists as microfauna, and different taxonomic groups of the mesofauna and macrofauna. It is known that these different levels of soil fauna respond to soil management and agricultural practices (Bedano et al., 2016; Xiong et al., 2017). The integration of this knowledge would give raise to a better understanding of the soil food web and could help to manipulate soil biology trough agricultural practices to enhance benefic soil animals that could act as controllers of pests. If this challenge is achieved the use of agrochemicals would be reduced and agricultural science could be one of the tools to act and mitigate the global climate change.

One way to increase ecosystem benefits would be through conservation agriculture (Derpsch et al., 2010, 2014; Albertengo et al., 2013). Within this type of soil management, no-till appears to be an important component of conservation agriculture, in opposition to conventional tillage, since the latter produces erosion and decreased soil health (Triplett and Dick, 2008). The loss of soil quality together with the need to produce more and better in a climate change context raise the need to make changes in the way of working land and producing from the ground.

Last but not least, an outstanding challenge is to put together ecological theory for macro-organisms and microorganisms. This fact has been elusive for scientists from both *words* and the simplest explanation is that the origin of both disciplines, ecology (plants and animals) and microbial ecology (bacteria, archaea, fungi and protists) started from very different mother disciplines. Naturalist disciplines as botany and zoology gave rise to ecology while reductionists disciplines as biochemistry and microbiology gave rise to microbial ecology. There were and there are important methodological limitations to study the microbial word, but as it was described before, this scenery has changed dramatically with the availability of molecular tools to analyze the microbial word. Recent efforts using coordinated protocols and new analytical methods allowed a huge metadata analysis on Earth microbiomes from different multiscale samples (Thompson et al., 2017). This communal catalogue of microbial diversity showed that agglomerative sampling can reveal basic biogeographic patterns of microbial ecology, with resolution and scope rivaling data compilations currently available for 'macrobial' ecology. It looks like the two distant worlds are becoming closer, and *ecology* will be only one for the scientists studying our living planet in the near future (Andrews, 2017).

9. Final remarks

Understanding which are the environmental determinants that shape the structure of the various soil microbiomes is expected to allow us to better understand soil functioning. It will help to change agriculture paradigm from the classical chemical one, in which soil is a mere large vase where the crops grow with good fertilizers, to a biological based one.

As described above, new molecular techniques revealed a new soil microbiology along with the beginning of the 21st century. The new techniques gave us new high-resolution pictures of completely unknown places. It is true that many things and histories can be read in a good photograph (Beceyro, 2003). But time is an essential part of life. So, may be not a photograph but a film is needed to explain the belowground life. But again, besides many films are like perfect descriptions of human life (Bergman, 1992), life is like a multidimensional film that we cannot enjoy from a comfortable sit, but instead enjoy it in an active way, being part of it.

10. Coauthors contributions

LGW, general idea and main writing; LAG, AEF, JPF, JC, DR and NBR, all of them have contributed with the analyses of particular references and general discussion.

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